

MORPHOLOGY AND DEVELOPMENT OF PISTILLATE INFLORESCENCES IN EXTANT AND FOSSIL CERCIDIPHYLLACEAE¹

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ABSTRACT

Comparison of the shoots, pistillate inflorescences, and infructescences of *Joffrea speirsii* Crane & Stockey from the upper Paleocene of Canada, *Nyssidium arcticum* (Heer) Iljinskaya from the upper Paleocene of southern England, and *Trochodendrocarpus arcticus* (Heer) Kryshstofovich from the lower Paleocene of Amur, eastern U.S.S.R., reveals considerable diversity in phyllotaxy, shoot growth, inflorescence position, and the number and crowding of follicles in each infructescence. Despite this diversity, the pistillate inflorescences of all these fossil *Cercidiphyllum*-like plants are directly comparable in basic organization, to inflorescences of extant *Cercidiphyllum*. These similarities add to the evidence that the fossil and extant taxa are closely related and support the view that the condensed inflorescence of *Cercidiphyllum* evolved by reduction from an elongated form. In extant *Cercidiphyllum* each flower consists of a single carpel, but in fossil taxa flowers may contain either one or two carpels. The arrangement of carpels in bicarpellate flowers resembles that in extant Hamamelidaceae.

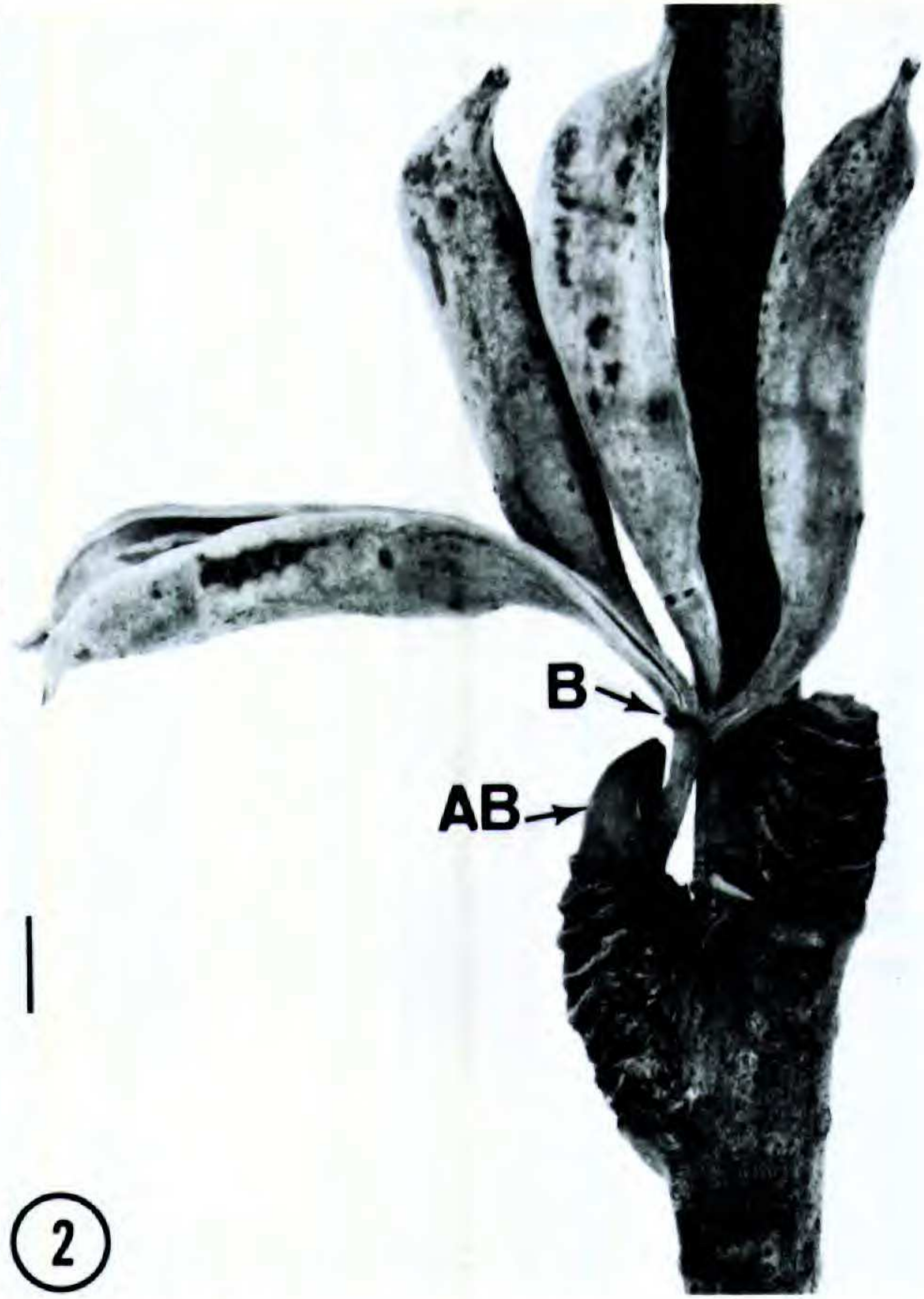
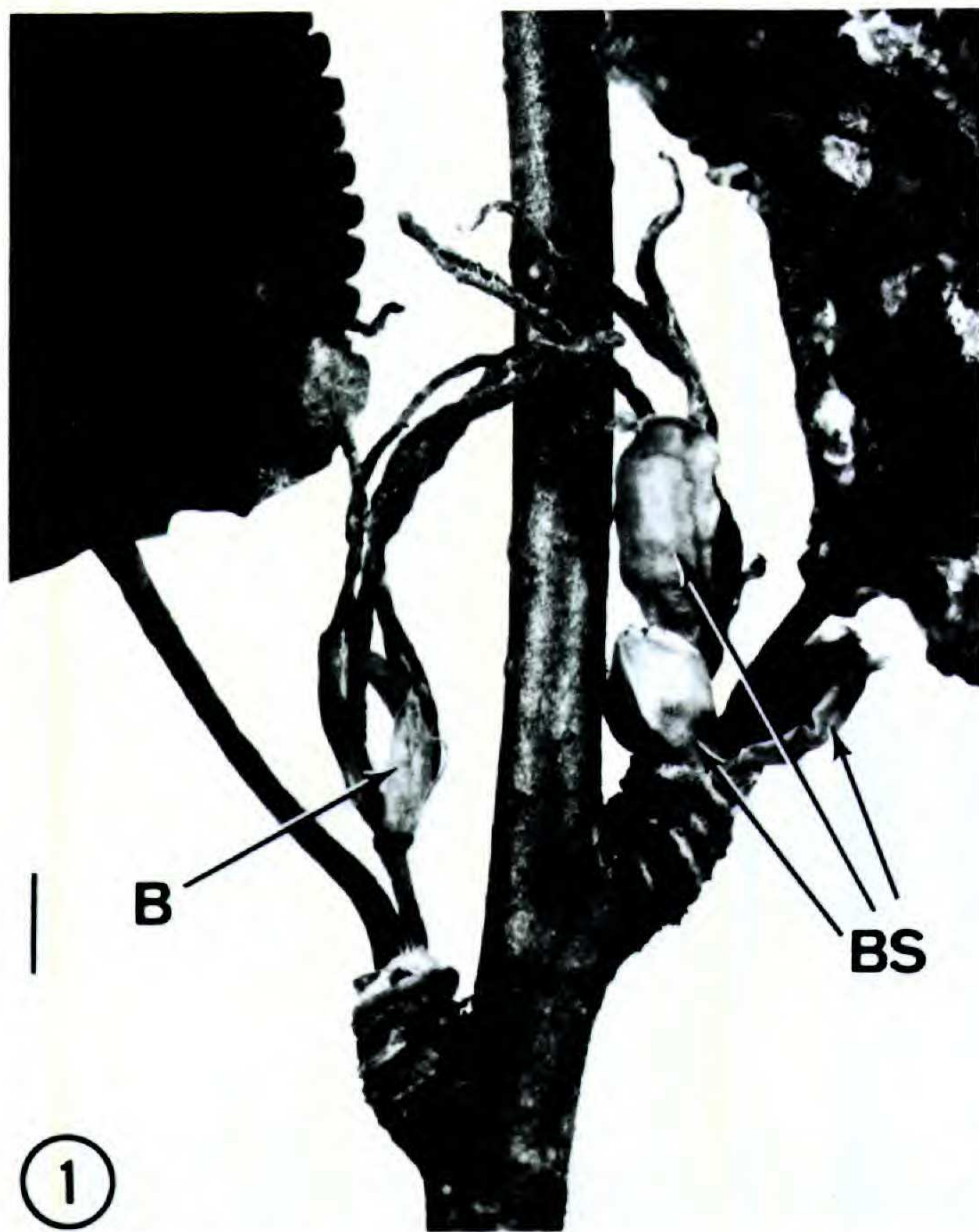
The Cercidiphyllaceae contain a single genus, *Cercidiphyllum*, with two very similar species of dioecious trees, *C. japonicum* Siebold & Zuccarini native to Japan and central and western China, and *C. magnificum* (Nakai) Nakai native to Honshu (Spongberg, 1979). The Cercidiphyllaceae have been placed in the Hamamelidales (Cronquist, 1981) or treated as a separate order, Cercidiphyllales, within the Hamamelidae (Takhtajan, 1969). *Cercidiphyllum* is thought to be "related on the one hand to the Hamamelidaceae (especially *Disanthus*) and on the other to the Trochodendrales and Magnoliales" (Cronquist, 1981: 167), although most authors agree that *Cercidiphyllum* is an isolated genus separated by large morphological gaps from its closest living relatives. The pistillate reproductive structures of *Cercidiphyllum* are unusual: they superficially resemble an apocarpous flower with two to eight carpels, but the carpel orientation is apparently anomalous, with the ventral suture directed abaxially. Swamy and Bailey (1949) supported the earlier hypotheses of Brown (1939), Harms (1916), and Solereder (1899), and inter-

preted the pistillate reproductive structure as a reduced inflorescence. As part of the evidence for this hypothesis Brown (1939) and Swamy and Bailey (1949) cited the elongated inflorescences of fossil *Cercidiphyllum*-like plants, which were widespread at middle and high latitudes of the Northern Hemisphere during the Upper Cretaceous and lower Tertiary (Brown, 1939, 1962; Chandrasekharam, 1974; Schloemer-Jäger, 1958). Although this hypothesis has been discussed by subsequent authors, the precise similarities between the fossil and extant inflorescences have remained obscure due to inadequate understanding of the fossil material. In recent years knowledge of these fossil plants has increased considerably (Crane, 1984; Crane & Stockey, 1985; Krassilov, 1976; Stockey & Crane, 1983). They are now known from seedlings, leaves, shoots, pistillate inflorescences, infructescences, seeds, and possible staminate inflorescences, and it is clear that these extinct *Cercidiphyllum*-like plants are more closely related to *Cercidiphyllum* than to any other genus (Crane & Stockey, 1985). In this paper we compare the

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FIGURES 1, 2. *Cercidiphyllum japonicum* Sieb. & Zucc.—1. Two short shoots with young pistillate inflorescences and leaves: note the long styles and stigmas, and three bud-scales (BS) surrounding the inflorescence and leaf on the right: inflorescence on left shows a bract (B) subtending one of the four carpels, $\times 3.5$.—2. Two curved short shoots showing leaf scars, axillary bud (AB), infructescence with four follicles, and bract scars (B) at base of follicles, $\times 3.3$. Scale bars, 2 mm.

shoots and pistillate reproductive structures of extant *Cercidiphyllum* with early Tertiary *Cercidiphyllum*-like plants from western Canada (*Joffrea speirsii* Crane & Stockey, 1985), southern England [*Nyssidium arcticum* (Heer) Iljin-skaya; Crane, 1984], and eastern U.S.S.R. [*Trochodendrocarpus arcticus* (Heer) Krysh-tovich; Krassilov, 1973, 1976]. The nomenclature for fossil taxa follows that adopted in Crane (1984), Crane and Stockey (1985), and Krassilov (1976). Discussion of the complex nomenclature and systematics of fossil *Cercidiphyllum*-like infructescences is outside the scope of this paper. Comparisons among fossil taxa demonstrate considerable diversity in phyllotaxy, shoot growth, inflorescence position, and the number and crowding of follicles in each infructescence. However, there are fundamental similarities in construction of the pistillate reproductive structures in the extant and fossil plants. These similarities add to the evidence that the fossil and extant taxa are closely related, explain some of the unusual morphological features of extant *Cercidiphyllum*, and facilitate more meaningful

comparison of the genus with other extant taxa in the Hamamelidae.

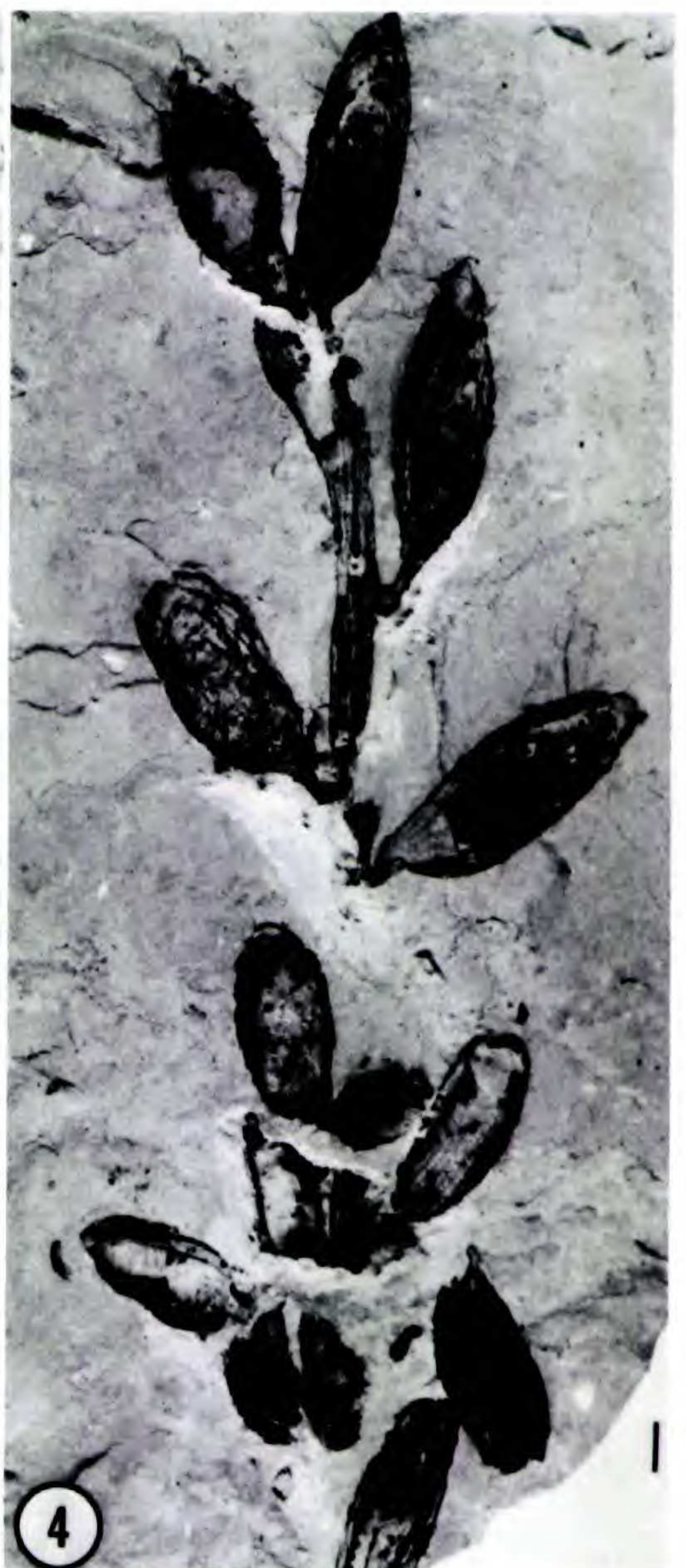
EXTANT *CERCIDIPHYLLUM*

Extant *Cercidiphyllum* has branches differentiated into long and short shoots. In trees that we have examined, long shoot leaves are opposite, subopposite, or occasionally in irregular whorls of three. Short shoots develop from the axillary buds of long shoot leaves. Each axillary bud has three bud-scales (Figs. 1, 19); the outer and inner are positioned opposite to the second bud-scale and the leaf of the preceding season. The new leaf develops opposite the inner bud-scale (Swamy & Bailey, 1949), and each short shoot bears a single leaf in each growing season (Fig. 1). Short shoot growth is sympodial, continuing each season through the activity of a new axillary bud. The resulting short shoots are distinctly curved toward the long shoot on which they are borne (Fig. 2).

In fertile short shoots the pistillate inflorescence is terminal and consists of a short axis that has a cluster of two to eight carpels at the apex



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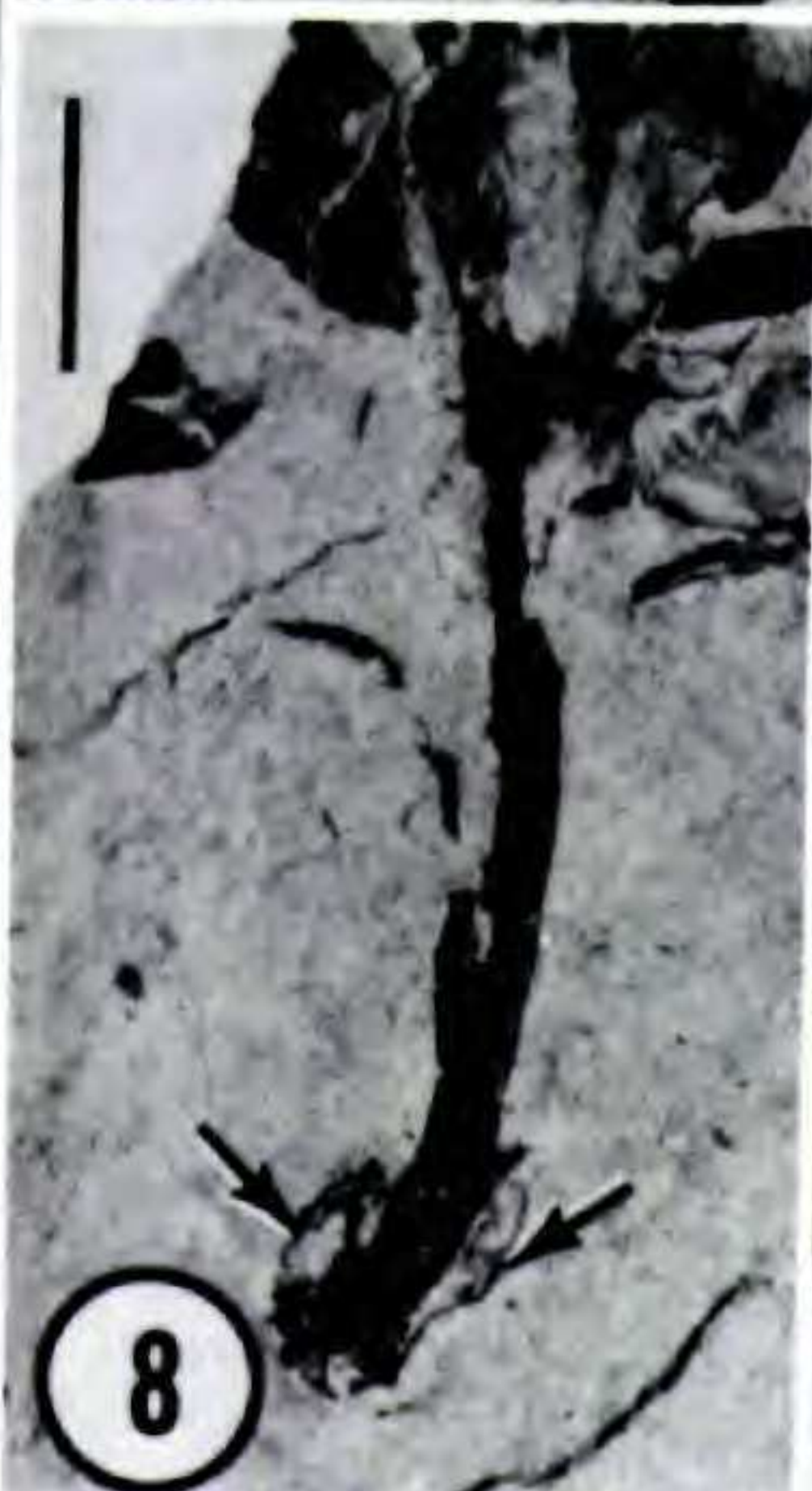
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(Figs. 1, 2). The carpels are arranged in opposite and decussate pairs, and the pairs are borne at slightly different levels (Swamy & Bailey, 1949). Each carpel is subtended by a membranous bract (Fig. 1) that is shed early in carpel development, leaving only a scar and sometimes a small flap of tissue at the base of the mature follicle (Fig. 2). The mature infructescence, including follicles, is up to 25 mm long. Attachment of pairs of carpels at different levels and the single bract associated with each carpel (Swamy & Bailey, 1949) are not consistent with the suggestion that the cluster of carpels is a simple apocarpous flower (Hutchinson, 1964). Each bract and the single carpel that it subtends are more readily interpreted as a single flower that lacks a perianth. The cluster of carpels is therefore an inflorescence of two to eight very simple flowers (Endress, 1986; Swamy & Bailey, 1949). The ventral suture of each carpel is oriented abaxially with respect to the inflorescence axis.

JOFFREA SPEIRSII CRANE & STOCKEY
(PALEOCENE, CANADA)

Joffrea speirsii Crane & Stockey, from the upper Paleocene, Paskapoo Formation of central Alberta, Canada (Crane & Stockey, 1985), is the most completely understood of all fossil *Cercidiphyllum*-like plants. *Joffrea* exhibits long and short shoot differentiation. Although the short shoots are often alternately arranged, leaf scars on the short shoots (Fig. 5) indicate that the leaves were borne in opposite and decussate pairs; an arrangement also clearly seen in the seedlings of *Joffrea* (Crane & Stockey, 1985; Stockey & Crane, 1983). The number of leaves borne on each short shoot in a single growing season is unknown. In *Joffrea* at least some short shoots bore two or more pistillate inflorescences at the apex (Fig. 3). Neither this nor the short shoot leaf arrangement

can be accounted for by sympodial growth. Together these features strongly suggest that short shoot growth was monopodial, with pistillate inflorescences developing from axillary buds of short shoot leaves.

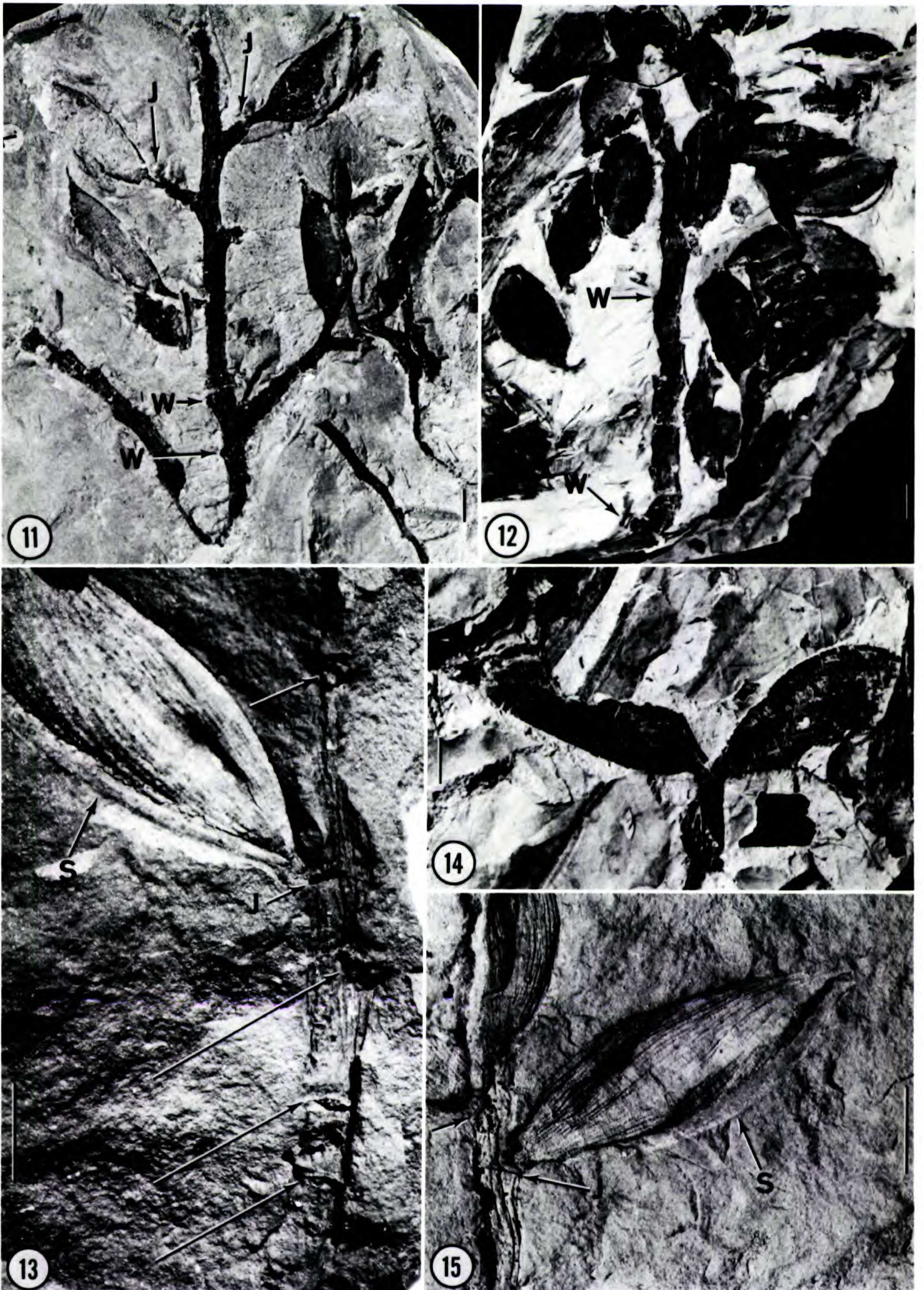
The pistillate inflorescence is elongated, up to 65 mm long, with bud-scales at the base (Figs. 3, 8). The inflorescence bears approximately 40 carpels spaced at intervals of 1–5 mm on short side branches of the inflorescence axis (Fig. 3). Each side branch bears one or two short-stalked carpels. The junction between the carpel stalk and the side branch of the inflorescence axis is marked by a distinct joint (Fig. 9), which may mark the attachment of a caducous bract as in extant *Cercidiphyllum*. Single carpels or pairs of carpels frequently have broken away from the inflorescence axis at this joint (Fig. 7). At maturity, the inflorescence elongated to approximately twice its original length, and the follicles were more widely spaced at intervals of 6–11 mm (Fig. 4). At this stage the joint at the base of the follicles is often difficult to detect; however, well-preserved impressions of similar (perhaps conspecific) infructescences from the upper Paleocene of Montana clearly illustrate this joint and the tendency of the follicles to break away at that point (Figs. 13, 15). *Joffrea* carpels that are borne singly have the ventral suture oriented adaxially with respect to the inflorescence axis, and carpels borne in pairs have the two sutures opposite each other (Figs. 6, 7). At maturity at least some of the single follicles twisted so that the ventral suture was oriented abaxially with respect to the inflorescence axis (Fig. 10).

NYSSIDIUM ARCTICUM (HEER) ILJINSKAYA
(PALEOCENE, ENGLAND)

Cercidiphyllum-like infructescences and follicles from the upper Paleocene Reading Beds

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FIGURES 3–10. *Joffrea speirsii* Crane & Stockey, from Red Deer, Alberta (Paskapoo Formation, upper Paleocene). All specimens (prefix S) in the University of Alberta Paleobotanical Collections (UAPC-ALTA).—3. Long shoot with attached short shoots: lower short shoot showing two attached pistillate inflorescences, a bud-scale (arrow), and an incomplete third axis or petiole (S11437A), $\times 1.6$.—4. Mature infructescence showing widely spaced follicles borne both singly and in pairs (S13357A), $\times 0.95$.—5. Short shoot showing diamond-shaped leaf scars: an opposite pair indicated with arrows (S13333), $\times 3.7$.—6. Ridged infructescence axis from which a pair of follicles have abscised: note sutures facing one another (S12358), $\times 1.75$.—7. Pair of carpels attached to a single stalk: note adaxial orientation of sutures with respect to floral axis, and remains of styles (S9191), $\times 2$.—8. Two bud-scales (arrows) at the base of a broken inflorescence (S12387), $\times 2$.—9. Inflorescence showing a distinct joint (arrow) at the base of a pair of follicles (S13323), $\times 2.8$.—10. Mature follicle showing twisted follicle stalk and abaxial orientation of suture with respect to infructescence axis (S12410B), $\times 2$. Scale bars, 4 mm.



FIGURES 11–15. *Cercidiphyllum*-like plants from the Paleocene of southern England and western North America. Specimens prefixed v. are from Berkshire, southern England (Reading Beds, Woolwich and Reading Formation, upper Paleocene) and are in the collections of the Department of Palaeontology, British Museum

(Woolwich and Reading Formation) of southern England were originally described as *Carpolithus gardneri* by Chandler (1961). The original specimens and additional material have recently been reexamined in detail (Crane, 1984) and assigned to *Nyssidium arcticum* (Heer) Iljinskaya. There is no evidence to suggest that the infructescences from the Reading Beds were borne on short shoots. The most informative specimens (Figs. 11, 12) suggest instead that the infructescences were borne as part of a long shoot system. These specimens exhibit whorls of oval scars that we interpret as leaf scars (Figs. 11, 12; see also Chandler, 1961). Growth in *N. arcticum* from the Reading Beds apparently resulted in the periodic production of whorls or pseudowhorls of leaves. Some leaf whorls are not followed by the production of an inflorescence (e.g., lower whorls, Figs. 11, 12). Other whorls of scars apparently delimit the base of infructescences (e.g., upper whorl, Fig. 11), and suggest that long shoot growth in this species was frequently terminated by the production of an inflorescence from the apical bud. Occasional branching occurred between the whorls of leaves, but the precise relationship of this to leaf and axillary bud production is not clear.

The pistillate inflorescences of *N. arcticum* from the Reading Beds are unknown, but the most complete infructescences are up to 130 mm long with about 15 widely spaced follicles approximately 5–6 mm apart. The follicles were borne singly (Fig. 11), or in pairs (Fig. 14), on short side branches of the infructescence axis (Crane, 1984). The best preserved specimen from the Reading Beds (Fig. 11) shows a distinct joint between the follicle stalk and the side branch of the inflorescence axis. Frequently this is not visible in poorly preserved material. However, other specimens indicate that follicles broke away from the infructescence axis at this point of

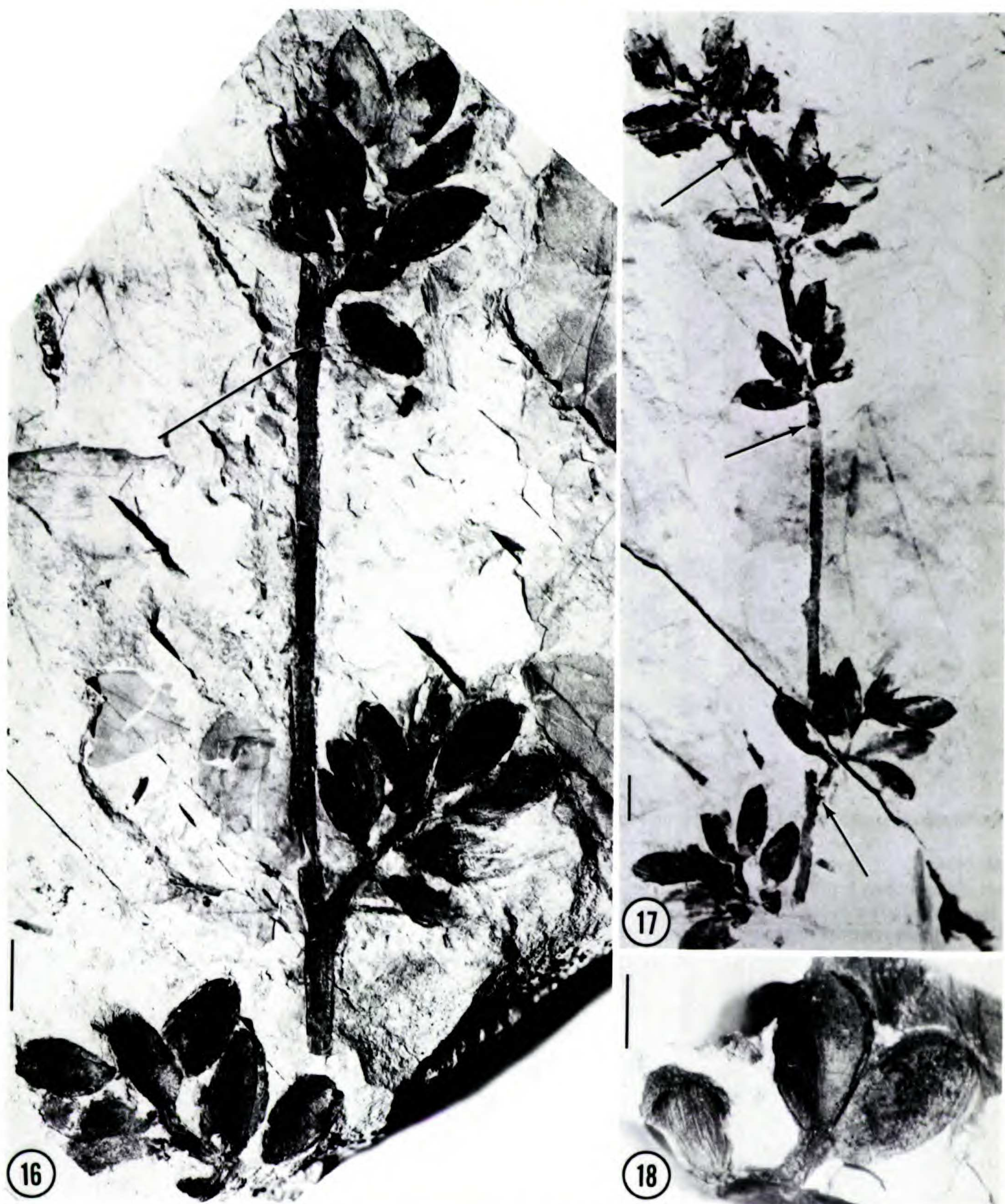
weakness (Fig. 14). As in *Joffrea*, the ventral sutures of pairs of follicles face each other. Suture orientation in single follicles is often unclear, but at least some were probably oriented abaxially with respect to the infructescence axis at maturity (Crane, 1984).

TROCHODENDROCARPUS ARCTICUS (HEER)
KRYSHTOFOVICH (PALEOCENE, U.S.S.R.)

Trochodendrocarpus arcticus (Heer) Kryshstofovich from the lower Paleocene (Danian) of Amur, eastern U.S.S.R. (Krassilov, 1973, 1976, 1977) is known from large specimens showing shoots that have attached infructescences. The infructescences are widely spaced and borne alternately, perhaps helically, on long shoots (Figs. 16, 17). A scar is often visible where each infructescence is attached to the long shoot (Figs. 16, 17). These scars are large and in the size range of petiole bases of associated *Cercidiphyllum*-like leaves. We suggest that the scars are those of alternate leaves and that each infructescence developed from an axillary bud. An alternative interpretation would be that each "infructescence" is a side branch of a large paniculate infructescence (Krassilov, 1977). This interpretation is more difficult to reconcile with the structure of other Paleocene *Cercidiphyllum*-like plants that are currently known.

The infructescences are up to 40 mm long and bear eight to 14 closely spaced follicles at distances of approximately 2–4 mm (Fig. 16). The follicles were borne singly (Krassilov, 1976, pl. 23: fig. 5) or in pairs (Fig. 18). None of the Amur material shows a distinct joint between the infructescence axis and the follicle stalk, although some of the dispersed follicles appear to have become detached at this point (Krassilov, 1976, pl. 24: fig. 9). The orientation of ventral sutures in the follicles is unclear.

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(Natural History). Specimens prefixed PP are from Decker, Montana (Tongue River Member, Fort Union Formation, upper Paleocene) and are in the paleobotanical collections of the Field Museum of Natural History, Chicago.—11. *Nyssidium arcticum* (Heer) Iljinskaya, long shoot with attached infructescences: note whorls of oval leaf scars (W) and distinct joint (J) between the follicles and infructescence axis (v.15336), ×1.—12. *N. arcticum*, long shoot with attached infructescence: note whorls of oval leaf scars (W) (v.60847), ×1.—13. *Cercidiphyllum*-like plant from Decker, Montana: note joint (J) between the follicle and infructescence axis, scars (arrows) where follicles have abscised, and the abaxial orientation of the follicle suture with respect to the infructescence axis (PP34177), ×3.—14. *N. arcticum* showing a pair of follicles attached to a common stalk (v.60851), ×1.5.—15. *Cercidiphyllum*-like plant from Decker, Montana, showing joint (J) between the follicle and the infructescence axis, and scar of an abscised follicle (upper arrow): note the abaxial orientation of the follicle suture with respect to the infructescence axis (PP34178), ×2.7. Scale bars, 5 mm.



FIGURES 16–18. *Trochodendrocarpus arcticus* (Heer) Krysh­tofovich from the lower Paleocene of Amur, U.S.S.R.—16. Long shoot with attached infructescences: note scar at arrow, $\times 1$.—17. Long shoot with attached infructescences: note scars at arrows, $\times 0.6$.—18. Pair of foli­cles with facing sutures attached to a common stalk, $\times 1$. Scale bars, 10 mm. Illustrations courtesy of V. Krassilov.

DISCUSSION

Shoot growth and phyllotaxy. *Cercidiphyllum* and its fossil relatives exhibit considerable variation in shoot growth. Long and short shoot differentiation is known in both *Joffrea speirsii*

and extant *Cercidiphyllum*, but these short shoots are of quite different types. Those of *Joffrea* are similar to those found in some gymnosperms (e.g., *Ginkgo*) and many flowering plants (e.g., *Prunus*), which involve small growth increments

of an otherwise normal monopodial shoot. The sympodial short shoots of *Cercidiphyllum* are more unusual and less common in flowering plants as a whole. The extant vesselless dicotyledon *Tetracentron sinense*, often interpreted as closely related to *Cercidiphyllum* (Takhtajan, 1969), also exhibits this unusual sympodial short shoot growth (Bailey & Nast, 1945; Nast & Bailey, 1945). In *Nyssidium arcticum* from southern England and *Trochodendrocarpus arcticus* from Amur, short shoots are unknown.

Phyllotaxy in the fossil and Recent plants is as diverse as shoot growth, ranging from alternate to opposite to whorled. Leaf morphology in extant *Cercidiphyllum* is extremely variable (Brown, 1939; Swamy & Bailey, 1949; Chandrasekharam, 1974) and is further complicated by pronounced differences between long and short shoot leaves. Latest Cretaceous and early Tertiary *Cercidiphyllum*-like leaves exhibit extreme variation in shape and venation (Hickey, 1977; Wolfe, 1966). Some of these leaves may have been produced by genera only distantly related to *Cercidiphyllum*, but much of the variation may also be accounted for by the wide range of shoot growth patterns and phyllotaxy in fossil *Cercidiphyllum*-like plants.

Inflorescence production and organization. Inflorescence production in *Cercidiphyllum* and its fossil relatives is highly variable (Table 1), but there is now a clear basis for directly interpreting the organization of the inflorescence in several fossil taxa in terms of the inflorescence of extant *Cercidiphyllum* (Figs. 19–24). In both the fossil and extant plants the inflorescence is a raceme. The joint between the branch of the inflorescence or infructescence axis and the stalk of the carpel or follicle is comparable to the joint at the base of each follicle in extant *Cercidiphyllum*. In extant *Cercidiphyllum* this joint marks the attachment point of a bract, and a bract may also have been borne at this point in the fossil plants (B, Figs. 19, 20). The joint is clear in *Joffrea* and *Nyssidium arcticum* but inferred in *Trochodendrocarpus arcticus*. The joint is also clearly visible in other early Tertiary material from North America (Figs. 13, 15), and we suggest that it was a general feature of Upper Cretaceous and early Tertiary *Cercidiphyllum*-like plants.

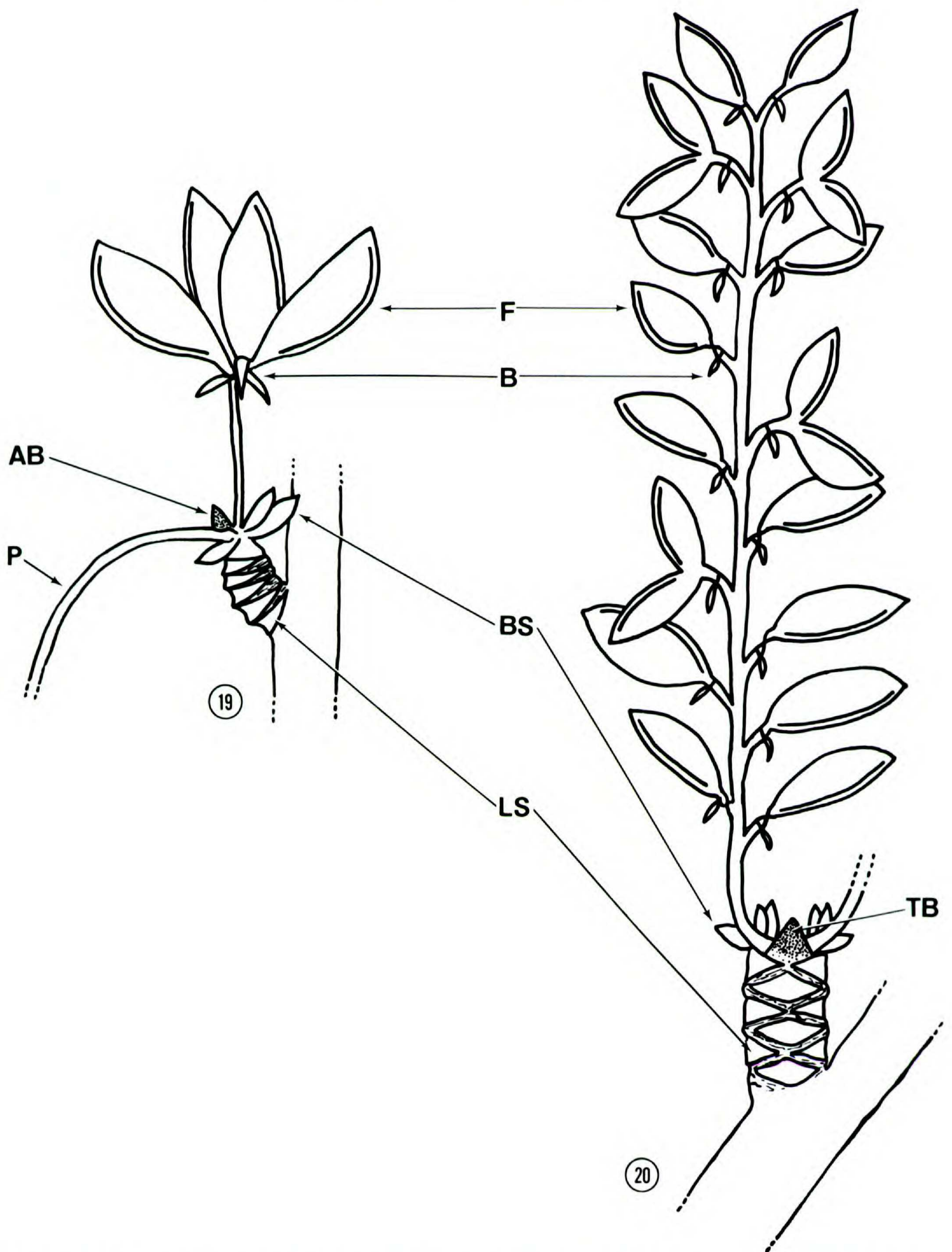
In *Joffrea speirsii* the base of the inflorescence has associated bud-scales (BS, Figs. 19, 20) that are comparable to those that surround the inflorescence, leaf and new axillary bud in extant *Cer-*

cidiphyllum. These bud-scales have not been seen in the fossil material from southern England or Amur.

Under the interpretation given above, the inflorescences of the fossil plants are directly comparable to the inflorescences of extant *Cercidiphyllum*, and the homologies hypothesized by Brown (1939) and Swamy and Bailey (1949) are supported and considerably clarified. The differences between the fossil and Recent inflorescences are principally quantitative and concern the interrelated factors of inflorescence length, follicle number, and follicle crowding.

Suture orientation. The orientation of the suture in fossil material has frequently been difficult to determine (Crane, 1984; Hickey, 1977), and discussions of this feature are complicated by the need to distinguish between suture orientation with respect to the inflorescence axis and suture orientation with respect to the floral axis. In *Joffrea*, suture orientation can be compared in both inflorescences and infructescences. At carpel stage all the sutures of single carpels are clearly adaxially oriented with respect to the inflorescence axis, but in paired carpels the sutures face each other and their orientation with respect to the inflorescence axis is unknown. At maturity the stalk of single follicles often twists to orient the suture abaxially with respect to the infructescence axis. This may be related to dispersal of seeds from the follicles (Crane & Stockey, 1985), and the same phenomenon may have occurred in other North American early Tertiary material (Brown, 1939, pl. 55: figs. 3, 10). In upper Paleocene material from Decker, Montana, single follicles also have the suture oriented adaxially with respect to the infructescence axis (Figs. 13, 15), but in these cases the lack of obvious twisting suggests that the suture orientation at carpel stage may also have been adaxial. The variability of suture orientation in different early Tertiary plants, combined with developmental changes, such as occur in *Joffrea*, probably account for the different suture orientations recorded in the literature (Basinger & Dilcher, 1983; Crane, 1984; Hickey, 1977).

Several explanations have been offered to account for the suture orientation in extant *Cercidiphyllum* (Harms, 1916; Hutchinson, 1964; Leróy, 1980; Solereder, 1899; Swamy & Bailey, 1949). Based on the interpretation of the *Cercidiphyllum* inflorescence as an apocarpous flower, Hutchinson (1964) suggested that the apparently abaxial suture orientation was anomalous



FIGURES 19, 20. Interpretative drawings showing homologous structures in the infructescences of *Cercidiphyllum* and *Joffrea*. — 19. *Cercidiphyllum japonicum* Sieb. & Zucc. Short shoot with infructescence. — 20. *Joffrea speirsii* Crane & Stockey. Short shoot with infructescence. AB = axillary bud, B = bract, BS = bud scale, F = foliule, LS = leaf scar, P = petiole, TB = terminal bud.

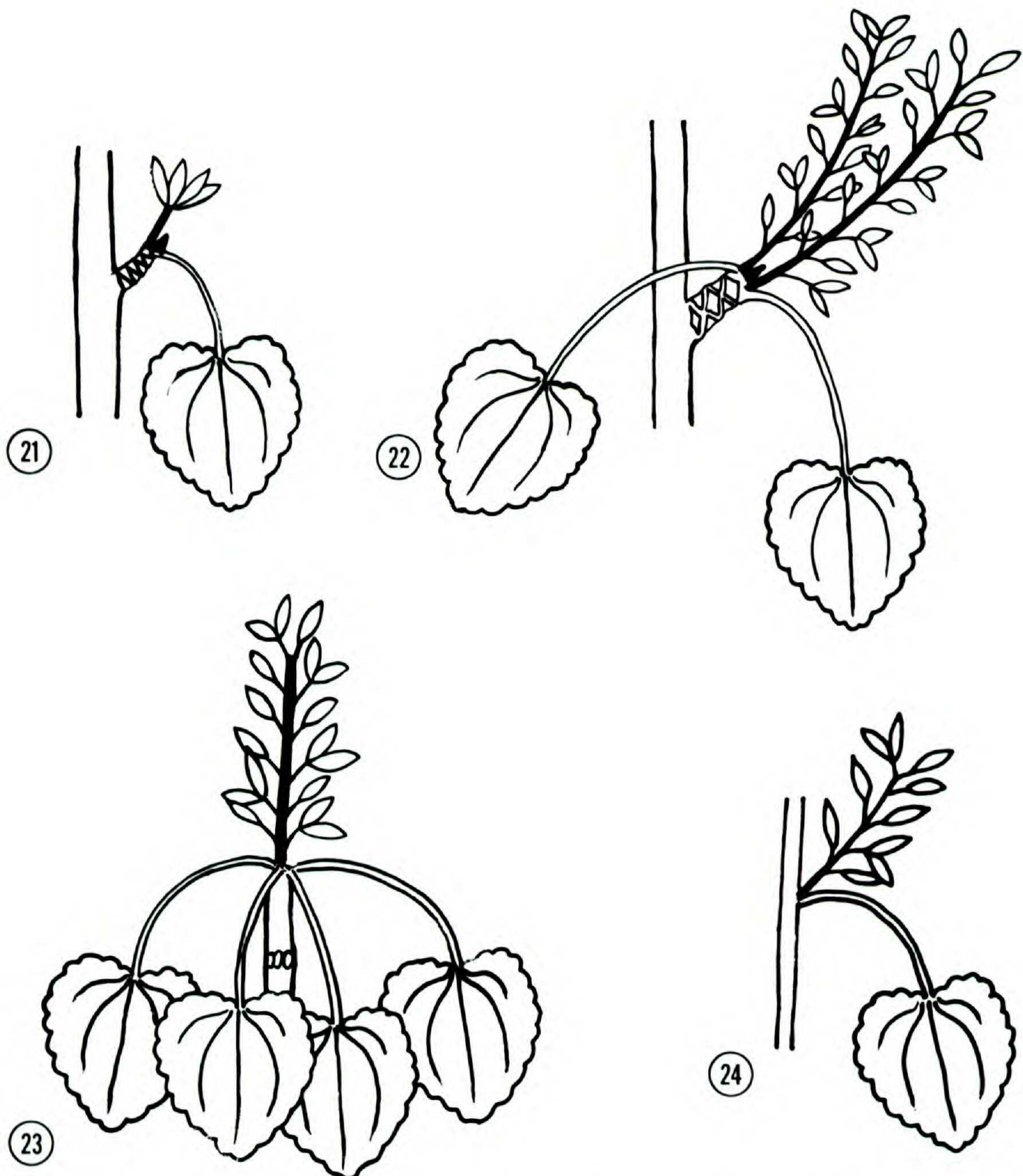
TABLE 1. Comparison of extant *Cercidiphyllum* with fossil *Cercidiphyllum*-like plants. See text for details of interpretations.

	<i>Cercidiphyllum</i> (Extant)	<i>Joffrea speirsii</i> (Paleocene, Canada)	<i>Nyssidium arcticum</i> (Paleocene, England)	<i>Trochodendro- carpus arcticus</i> (Paleocene, U.S.S.R.)
Shoots	Long shoots, sympodial short shoots	Long shoots, monopodial short shoots	Long shoots, short shoots absent?	Long shoots, short shoots absent?
Phyllotaxy	Opposite, subopposite, or whorled on long shoots, single on short shoots	Opposite (occasionally alternate?) on long shoots, opposite on short shoots	Whorls or pseudowhorls	Alternate
Position of inflorescence	Terminal on sympodial short shoots	In leaf axils on monopodial short shoots	Terminal on long shoots	In leaf axils on long shoots
Inflorescence type	Raceme	Raceme	Raceme	Raceme
Maximum length of infructescence	25 mm	130 mm	130 mm	40 mm
Follicle number per infructescence	2–8	ca. 40	ca. 15	8–14
Follicle orientation with respect to infructescence axis	Always abaxial	Single follicles, adaxial initially, some twisted and abaxial at maturity; unknown in paired follicles	Single follicles, ?adaxial, some abaxial at maturity; unknown in paired follicles	Unknown
Follicle number per flower	Always 1	1 or 2	1 or 2	1 or 2
Follicle orientation with respect to floral axis ^a	?Adaxial	?Adaxial, certainly adaxial when paired	?Adaxial, certainly adaxial when paired	Unknown

^a Follicle orientation with respect to floral axis is difficult to assess in unicarpellate flowers.

and due to twisting of the carpels. This is not supported by detailed developmental studies or by carpel and follicle vasculature (Swamy & Bailey, 1949). The complex explanations of Harms (1916) and Leróy (1980) both involve transformation of a bud-scale on a vegetative shoot into a carpel, the single leaf of the shoot being transformed into a bract (Harms, 1916) or being lost (Leróy, 1980). Solereder's (1899) view is more straightforward, simply involving the loss of one of a pair of carpels that originally had opposite ventral sutures (adaxial with respect to the floral axis) and were oriented perpendicular to the inflorescence axis. This interpretation receives some

support from the variable vascular supply to *Cercidiphyllum* carpels: some carpels have the dorsal vein supplied by a single vascular bundle from the stele, whereas others are supplied by two vascular bundles which fuse in the base of the carpel (Swamy & Bailey, 1949: 192, fig. 12). Equally significant however is the regular occurrence of pairs of follicles that have opposite ventral sutures in the inflorescences of *Joffrea*, *N. arcticum*, and *T. arcticus* (Figs. 6, 7, 14, 18). Although it is unknown whether the paired carpels and follicles are perpendicular or transverse with respect to the inflorescence axis, in all other respects the fossil plants conform to the archetype



FIGURES 21–24. Interpretative summary drawings showing shoot morphology, phyllotaxy, and infructescence position in extant and fossil *Cercidiphyllaceae*.—21. *Cercidiphyllum japonicum* (extant), showing sympodial short shoot with a single leaf, axillary bud, and terminal infructescence.—22. *Joffrea speirsii* (Paleocene) showing monopodial short shoot with opposite and decussate leaves, terminal bud, and axillary infructescences.—23. *Nyssidium arcticum* (Paleocene) from southern England showing long shoot with whorled leaves and terminal infructescence.—24. *Trochodendrocarpus arcticus* (Paleocene) from Amur showing long shoot with alternate leaves and an axillary infructescence.

of extant *Cercidiphyllum* envisaged by Solereder. Fossil infructescences more similar to those of extant *Cercidiphyllum* are first recorded from the Oligocene (Jähnichen et al., 1980).

CONCLUSIONS

Extinct latest Cretaceous and early Tertiary *Cercidiphyllum*-like plants are very diverse in phyllotaxy, shoot growth, pistillate inflorescence production, and the number and crowding of follicles per infructescence (Figs. 21–24). This extreme morphological diversity emphasizes that

the complex of plants that produced *Cercidiphyllum*-like leaves during the latest Cretaceous and early Tertiary was highly heterogeneous, and further variations other than those considered here remain to be described in detail (Basinger & Dilcher, 1983). Extreme caution will therefore be necessary in assigning isolated and poorly understood organs of these *Cercidiphyllum*-like plants either to the extant genus or to already established and relatively well understood fossil plants such as *Joffrea*. The precise systematic relationships among these fossil plants remain to

be resolved by detailed studies of well-preserved inflorescences and shoots. Nevertheless, despite the structural diversity of *Cercidiphyllum*-like plants, the direct comparability of the inflorescences of extant *Cercidiphyllum* to those of the fossil *Cercidiphyllum*-like plants is now established. The fossils also provide support for the hypothesis that the suture orientation in extant *Cercidiphyllum* is due to loss of one of a pair of opposite carpels. The suture in extant *Cercidiphyllum* is therefore abaxial with respect to the inflorescence axis but probably phylogenetically adaxial with respect to the floral axis of the "ancestral" flower.

The recognition that bicarpellate flowers may be the primitive condition in the Cercidiphyllaceae strengthens the idea that the family may be closely related to the Hamamelidaceae (Cronquist, 1981). The close resemblance among the infructescences of *Joffrea*, *Nyssidium*, and *Trochodendrocarpus* and the racemes of unisexual, often apetalous, bicarpellate flowers seen in *Sinowilsonia* (Hamamelidaceae, Endress, 1977) is particularly striking. The phylogenetic relationships between the extant and fossil Cercidiphyllaceae and Hamamelidaceae deserve detailed study aimed at determining whether bicarpellate flowers constitute an important defining character for this group.

LITERATURE CITED

- BAILEY, I. W. & C. G. NAST. 1945. Morphology and relationships of *Trochodendron* and *Tetracentron*, I. Stem, root, and leaf. *J. Arnold Arbor.* 26: 143–154.
- BASINGER, J. F. & D. L. DILCHER. 1983. Fruits of *Cercidiphyllum* from the early Tertiary of Ellesmere Island, arctic Canada. *Amer. J. Bot.* 70(5, 2): 67. [Abstract.]
- BROWN, R. W. 1939. Fossil leaves, fruits and seeds of *Cercidiphyllum*. *J. Paleontol.* 13: 485–499.
- . 1962. Paleocene flora of the Rocky Mountains and Great Plains. *Profess. Pap. U.S. Geol. Surv.* 375: 1–119.
- CHANDLER, M. E. J. 1961. The Lower Tertiary Floras of Southern England, I. Palaeocene Floras: London Clay Flora (Supplement) & Atlas. British Museum (Natural History), London.
- CHANDRASEKHARAM, A. 1974. Megafossil flora from the Genesee locality Alberta, Canada. *Palaeontographica, Abt. B, Paläophytol.* 147: 1–41.
- CRANE, P. R. 1984. A re-evaluation of *Cercidiphyllum*-like plant fossils from the British early Tertiary. *Bot. J. Linn. Soc.* 89: 199–230.
- & R. A. STOCKEY. 1985. Growth and reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the Late Paleocene of Alberta, Canada. *Canad. J. Bot.* 63: 340–364.
- CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- ENDRESS, P. K. 1977. Evolutionary trends in the Hamamelidales-Fagales group. *Pl. Syst. Evol. Suppl.* 1: 321–347.
- . 1986. Floral structure, systematics and phylogeny in Trochendrales. *Ann. Missouri Bot. Gard.* 73: 297–324.
- HARMS, H. 1916. Über die Blütenverhältnisse und die systematische Stellung der Gattung *Cercidiphyllum* Sieb. & Zucc. *Ber. Deutsch Bot. Ges.* 34: 272–283.
- HICKEY, L. J. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. *Mem. Geol. Soc. Amer.* 150: 1–293.
- HUTCHINSON, J. 1964. The Genera of Flowering Plants, Dicotyledons, I. Clarendon Press, Oxford.
- JÄHNICHEN, H., D. H. MAI & H. WALTHER. 1980. Blätter und Früchte von *Cercidiphyllum* Siebold & Zuccarini im mitteleuropäischen Tertiär. *Schriftenreihe Geol. Wiss.* 16: 357–399.
- KRASSILOV, V. A. 1973. Mesozoic plants and the problem of angiosperm ancestry. *Lethaia* 6: 163–178.
- . 1976. The Tsagayan Flora of Amur Region. Nauka, Moscow. [In Russian.]
- . 1977. The origin of angiosperms. *Bot. Rev. (Lancaster)* 43: 143–176.
- LERÓY, J. F. 1980. Développement et organogenèse chez le *Cercidiphyllum japonicum*: un cas semblant unique chez les Angiospermes. *Compt. Rend. Hebd. Séances Acad. Sci. Sér. D*, 290: 679–682.
- NAST, C. G. & I. W. BAILEY. 1945. Morphology and relationships of *Trochodendron* and *Tetracentron*, II. Inflorescence, flower, and fruit. *J. Arnold Arbor.* 26: 267–276.
- SCHLOEMER-JÄGER, A. 1958. Alttertiäre pflanzen aus Flözen der Brögger-Halbinsel Spitzbergens. *Palaeontographica, Abt. B, Paläophytol.* 104: 39–103.
- SOLEREDER, H. 1899. Zur Morphologie und Systematik der Gattung *Cercidiphyllum* Sieb. & Zucc., mit Berücksichtigung der Gattung *Eucommia* Oliv. *Ber. Deutsch Bot. Ges.* 17: 387–406.
- SPONGBERG, S. A. 1979. Cercidiphyllaceae hardy in temperate North America. *J. Arnold Arbor.* 60: 367–376.
- STOCKEY, R. A. & P. R. CRANE. 1983. In situ *Cercidiphyllum*-like seedlings from the Paleocene of Alberta, Canada. *Amer. J. Bot.* 70: 1564–1568.
- SWAMY, B. G. L. & I. W. BAILEY. 1949. The morphology and relationships of *Cercidiphyllum*. *J. Arnold Arbor.* 30: 187–210.
- TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Oliver & Boyd, Edinburgh.
- WOLFE, J. A. 1966. Tertiary plants from the Cook Inlet Region, Alaska. *Profess. Pap. U.S. Geol. Surv.* 398B: 1–32.